Practice Catches Theory in Kin Recognition

Burgeoning laboratory and field studies are beginning to focus on the mechanisms by which even the lowliest animals recognize their kin

Kinship has long been a prominent thread of human social fabric, and it is often woven into the most complex of patterns. So fundamental to human behavior is the phenomenon that the ability to recognize kin as kin, which clearly must underlie the whole structure, is barely raised to the level of consciousness. So, too, with other animals. From tadpoles to monkeys, bees to ground squirrels, the ability to discriminate between kin and nonkin has in recent years been demonstrated to occur in many levels of the animal world.

Although the degree of sophistication of interaction between relatives in the "lower" animals is more modest than that among humans, there turns out to be surprising layers of subtlety. For instance, tadpoles of American toads can apparently discriminate between siblings and nonsiblings, even though they themselves have been reared alone. And Belding's ground squirrels know the difference between full-sibs and half-sibs, even when they are all reared together in the same burrow.

Two general questions immediately raise themselves in regard to kin recognition in animals other than humans: why? and how? The first question addresses the benefits to individuals that might accrue from being able to discriminate between relatives and nonrelatives and to assess extent of relatedness too. The second would examine the mechanisms by which animals categorize individuals with whom they interact. This is not to imply that organisms make conscious assessments of relatedness, but that, as Paul Sherman of Cornell University puts it, "They just behave as if they do." The "how?" question is currently receiving most of the attention.

Interest in kin recognition—specifically parent (usually mother)/infant interaction—has a long history, although it has only relatively recently been conceived in these terms. Konrad Lorenz's classic work on imprinting, in which, say, a gosling, becomes fixated upon the first object it espies after emerging from the shell, is encompassed by kin recognition, although initially it was thought of as a species recognition process. "I realized it wasn't a species recognition process, but instead had to do with individual recognition," recalls Patrick Bateson, of the University of Cambridge, England. "You surely don't need mechanisms of that sort for species recognition. After all, a cuckoo grows up in a nest in the company of different species, and yet has no difficulty in recognizing its own species later as an adult."

Bateson made these observations in a review written in 1966, but it was to be some while before individual recognition in general and kin recognition in particular were to become common currency. It has become obvious to biologists since then that kin recognition is important in four major areas. The first is the ability of parents to recognize their offspring and so avoid squandering resources through rearing unrelated young. The second, which follows from this one, is the need of young to recognize their parent and so avoid being harmed through approaching a nonparent adult. (The classical imprinting is the operative mechanism here.) The third and fourth areas—termed kin selection and mate choice, respectively—have formed the principal thrust to kin recognition work during the past decade.

In 1964 William Hamilton, then at Imperial College, London, published a significant refinement of the theory of natural selection. An individual's fitness (in Darwinian terms) could be counted not just in terms of the number of its own offspring, he said, but also in the reproductive success of near relatives, because near relatives share substantial portions of their genome. By helping close kin, an individual might increase its "inclusive fitness," so called.

It was to be some while before the import of Hamilton's thesis was appreciated, and still longer before it was tested. "It took field biologists about 10 years before they could quantitatively ask the questions implied by Hamilton's work," comments Sherman. "Specifically, if, for whatever reason, animals live in social groups there will be an opportunity for kin selection to operate. Nepotism depends on the ability of individuals to discriminate between kin and nonkin. The problem with studying this, however, is that building up marked populations of known kin takes many years."

During this same period there developed a parallel interest in kin recognition, which had to do with the way individuals chose suitable mates. The dangers of reduced genetic fitness through close inbreeding and the threat of losing adaptive genetic complexes through too much outbreeding frequently occupy the thoughts of population

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Baboons, Kenya

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Belding's ground squirrels

Although these ground squirrels appear not to discriminate between their nestmates while still young, by the time the females reach one year they are able to recognize full-sibs as against half-sibs. Two mechanisms of kin recognition appear to be operating here: first, association, during the early stages of life; and then phenotype matching in later life.

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geneticists; and, judging by a rapidly growing body of evidence, nonhuman animals have an interest too. Animals tend to choose as mates first cousins rather than siblings or more distantly related individuals. Bateson terms the compromise between these two hazards "optimal outbreeding." By contrast, William Shields, of the State University of New York, Syracuse, prefers the term "optimal inbreeding." In any case, Bateson has obtained experimental data on Japanese quail that indicate that the birds are able to assess relatedness of potential mates with some sensitivity.

Initially this twin thrust was dominated by an enchantment with kin selection. Moreover, when evidence of kin recognition was obtained—as it quickly was, in insects, amphibians, birds, and mammals—its apparent confirmation of kin selection theory was often taken as an end in itself. Now, however, there is an expanding emphasis on the mechanisms of kin recognition and a growing realization that the true benefits of the ability—whatever they might be—must be conceptualized and measured much more carefully than hitherto. "There is alot of straightforward field work and ecology to be done," says Bateson.

Mechanisms of kin recognition as currently understood fall into four categories, with one of them being little more than an interesting though unlikely theoretical possibility.

The first, known as spatial distribution, applies, for instance, when a parent bird nurtures its prefledgling offspring in its nest. The adult cues on the nest rather than the specific individuals within it, and individual recognition begins only when the young emerge from the nest. At this prefledgling state a Franklin's gull, for instance, will accept other chicks in her nest as her own and will ignore a true offspring that is outside the nest. When the offspring have fledged, the recognition pattern is reversed.

The second form of kin recognition, called association, appears to be the most common in nature. Simply, one young will accept as siblings other young with which it is reared. This is obviously a form of imprinting, and there is now a great body of data demonstrating its existence and importance.

A third possible mechanism invokes putative recognition alleles and appears as yet to have little theoretical backing and less experimental support. Hamilton raised the possibility early on and suggested that a gene might be responsible for both the expression of a specific trait and the recognition of that trait in others. Richard Dawkins, a biologist at Oxford University, England, calls it the green beard effect: put simply, it says "I have a green beard and I will be altruistic to anyone else with a green beard."

There are theoretical reasons why recognition alleles might be evolutionarily unstable and practical reasons why it is very difficult to envisage a gene or gene complex mediating both the expression of a trait and its detection in others. "Naïve," is how Bateson describes it. Nevertheless, he does note that this type of mechanism might operate in cell/cell recognition, and something of the sort might be possible in olfactory systems. One tantalizing piece of experimental evidence is the apparent ability of mice to detect a single gene change (in the major histocompatibility complex) in an otherwise genetically identical partner. "No one knows how this works."

The fourth mechanism, which is termed phenotype matching, is currently the subject of most interest. Sherman, who coined the term jointly with Warren Holmes, of the University of Michigan, in an article in 1982, says it is "a system that evolves where the others don't work." An animal learns what a relative should look like, by, say, using itself or its mother as a referent, and then categorizes others according to how they match with this template phenotype. It is a learning process of the type that psychologists have for years called stimulus generalization. As a kin recognition mechanism, phenotype matching depends on the reasonable supposition that degree of genetic distance is reflected in degree of phenotypic similarity.

The simpler mechanisms of spatial distribution and association fall down, says Sherman, "where an individual is not related as it appears to be." A good example, on which Sherman and his colleagues have been working, is the Belding's ground squirrel. Females are typically fertilized by more than one male, and so the litters are typically a mixture of full- and half-sibs. With the association mechanism operating, all would treat each other as full-sibs, and this is what appears to occur, at least until the young begin to mature.

By the time the young ground squirrels are a year old the females, which usually remain in their natal area and are therefore often in contact with their mother and sisters, are able to discriminate between full- and half-sibs. By contrast, males, which usually disperse from their natal area and therefore have little further contact with their kin, apparently do not make this discrimination. This difference between dispersing males and sedentary females fits neatly with kin selection theory, which would predict a greater kin assessment ability in the sex that interacts frequently with its relatives.

Building on earlier theoretical treatments by Hamilton and Richard Alexander, of the University of Michigan, Sherman and Holmes identify a number of social and ecological circumstances in which phenotype matching might be expected to evolve. For instance, situations other than polygamy in which nestmates might not be full-sibs occur with cooperative breeding, where young of several females are reared in one site and with the deposition in the nest of the young of either the same species or possibly of another species. In addition, if individuals that disperse from a natal site are likely to encounter kin in adult life there would be an advantage in recognizing them. "You can imagine the immense problems with field observations of this kind of situation," comments Sherman.

According to Holmes, the Belding's ground squirrels appear to use perception of self as a template for phenotype matching, as, incidentally, do the tadpoles of the American toads, which have been studied by Bruce Waldman, also at Cornell. By contrast, Les Greenberg, of Texas A&M University, has shown that female sweat bees, which guard against intruders to their nest, use their nestmates as a template. If a female is reared in a nest with unrelated individuals it will allow access to the nest to these individuals and to the sisters of these individuals, with which it has had no previous contact.

The big question about phenotype matching is, how does it operate? What cues—visual, olfactory, oral, and so on—are involved? And what is the genetic basis? Bateson suspects that the pattern recognition process involved is generally exceedingly complicated. "When you know what the cues are, you can begin to manipulate them," he says. "But none of us knows in any detail what we are dealing with, beyond saying it is visual in one case, for instance, and olfactory in another."

In a theoretical exercise on the possible genetic parameters of kin recognition with Robert Lacy, of Franklin and Marshall College, Lancaster, Pennsylvania, Sherman appears to confirm all too depressingly the complexity of the system. "For example," they write, "34 independently assorting genetic loci with two alleles each are required for full-sib/nonrelative discrimination with a 10% probability of error." Full-sib/half-sib and half-sib/nonrelative discrimination require 66 and 404 traits, respectively, all of which implies an immense amount of genetic information.

An interesting twist on the perception of the phenomenon of kin recognition as a putative specific example of a general method of learning comes from work by Bateson and fellow Cambridge biologist Gabriel Horn. By ablating a tiny part of the chick forebrain—the intermediate part of the medial hyperstriatum ventral (IMHV)—before the bird has been exposed to any imprinting stimuli, it is possible to prevent imprinting from occuring. Similarly, ablation following imprinting more or less expunges the preference that had been acquired.

The intriguing part of these observations is that although imprinting is affected by the procedure, other learning processes are not. This observation implies that this mechanism of kin recognition is a rather specific form of learning, one perhaps designed to protect under normal circumstances a very special and important function. No neurological information exists for other species on this issue, beyond the striking clinical observation that a patient whose IMHV has been damaged in some way has a specific inability to recognize faces.

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What Is the Risk from Chlorofluorocarbons?

A new Academy report predicts a reduced risk of danger to ozone, but only if certain questionable assumptions are made

The new report from the National Academy of Sciences (NAS) to the Environmental Protection Agency about the potential danger to the ozone layer from chlorofluorocarbons* has some good news and some bad news. The good news is a modest lowering in the predicted depletion of atmospheric ozone as a result of the continued release of chlorofluorocarbons into the environment. The bad news is that the prediction is based on at least one major assumption that may no longer be true.

Furthermore, that modest decrease in atmospheric ozone is actually the result of what Herbert Kaufman of the University of Pittsburgh terms "a precarious balance" between a dramatic decrease in ozone concentrations in the upper atmosphere and an equally large increase at lower altitudes. This rearrangement of atmospheric ozone has the potential to become as troubling as a sharp depletion in stratospheric ozone might have been. The potential hazards are much more complicated than it would appear at first blush.

The most important chlorofluorocarbons (CFC's, often known by the trade name Freons) are CFC-11 ($CFCl_3$) and CFC-12 (CF_2Cl_2). The use of CFC's in aerosols was banned in 1977, but they are still widely used as refrigerants and as foaming agents for polymers. When they are eventually released to the atmosphere, their inertness to most biological processes allows them to be transported to the stratosphere, where they are broken down by sunlight. Liberated chlorine catalytically destroys ozone, which acts as a shield against the sun's ultraviolet radiation. It has been estimated that each 1 percent depletion in ozone would increase the amount of ultraviolet light that reaches the earth's surface by 1 to 3 percent, and that such increases could produce deleterious consequences ranging from decreases in food production to increases in the incidence of cancer.

The projected risk to atmospheric ozone has been reduced with successive reports from the Academy. A 1979 report estimated an eventual depletion of 18.6 percent if release of CFC's continued at the 1977 rate. A 1982 report (*Science*, 23 April 1982, p. 396) predicted a depletion in the range of 5 to 9 percent if emissions continued at the same rate. The new report reduces that estimate still further, to 2 to 4 percent. The changes in the projections arise from two major sources: improved values for rate constants for certain reactions in the atmosphere and the inclusion of other trace gases in the mathematical models used to make the projections.

The determination of rate constants has been a particularly vexing problem. There are at least 192 chemical reactions and 48 photochemical processes that occur in the stratosphere, although only about 150 or fewer of these parameters are actually used in most modeling calculations. Most of those reactions are very fast processes involving highly reactive species, particularly free radicals and atoms in excited states, whose reactions can affect the chemistry of the stratosphere at very small concentrations.

Many of these reactions are very difficult even to reproduce in the laboratory, much less to measure their rates. Determination of those rates has required the development of sophisticated laser-based techniques both for initiating the reactions and for determining the rates. By sheer coincidence, most of the recent refinements in rate constants have tended to reduce the predicted depletion.

The report cites at least six different reactions whose rate constants have recently been revised dramatically. One example is the reaction

$$O + HO_2 \rightarrow OH + O_2$$

which removes odd oxygen atoms while converting hydroperoxide into the more reactive hydroxyl radical, which in turn reduces the concentration of ozone in the upper stratosphere. Working with such radical-radical reactions in the past has been very difficult because both highly reactive species must be produced and monitored accurately and sensitively. In 1983, three separate groups used

**Causes and Effects of Changes in Stratospheric Ozone: Update 1983* (National Academy Press, Washington, D.C., 1984).